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X

COLOR CHANGES AND STRUCTURE OF THE SKIN OF ANOLIS CAROLINENSIS

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The mechanism of the color changes in the lacertilia has been the subject of much investigation, especially in that of the African Chameleon. One need only refer to the works of Brücke, Keller, and Fuchs for historical resumés. Brücke, Pouchet, and Keller have attempted to solve this problem by a close study of the histological structure of the skin and Keller was able to demonstrate clearly the various elements essential for the production of the various color states.

The histological structure of the skin of Anolis has, as far as I have been able to determine, been studied only by Carlton, who attempted to correlate the findings of Keller in the chameleon with those in Anolis.

The *Anolis carolinensis*, or so-called Florida Chameleon, belongs to the family Iguanidæ and is in no way related to the true chameleons. Its habitat is the southeastern part of the United States and Cuba. It may be distinguished from all other North American lizards except the Geckos, according to Ditmars, by the expanded and flattened adhesive pads on the middle four phalanges of each foot.

It is entirely insectivorous, subsisting mainly on flies and meal worms, which it is able to capture with almost unerring accuracy. Water in the form of scattered droplets is lapped by means of its thick tongue and these lizards soon become dehydrated and die if water be not supplied in this form.

A characteristic flattened, semicircular projection of the skin, known as the throat-fan (Ditmars), dewlap or gular appendage

(Gadow), is produced at will in the mid-ventral region of the head and neck. This fan is produced by the hyoidean apparatus. The mechanism of this apparatus consists of a double, tapering cartilage lying in the mid-ventral line and attached to the body of the hyoid just anterior to a line through the center of the eye. When erected, it carries the loose skin of the cervical region with it.

This throat-fan is, according to Ditmars, purely ornamental and produced only by the males, being accompanied by a vigorous nodding of the head and neck.

It is produced when a male spies a female or when it prepares for combat with another male. When the males are captured and held in the hand, this fan becomes prominent. Often when two males meet, each one will erect a ridge along the mid-dorsal line extending from the base of the occiput to a variable distance along the back. This may be accompanied by a marked lateral compression of the thorax and abdomen so that the lateral diameter is smaller than the dorso-ventral, whereas under ordinary conditions the reverse is true. The throat-fan is usually very prominent during this state and there is present a characteristic coloration which will be described later.

The Anolis lives well in captivity when supplied with water in the form of scattered droplets and flies or meal worms. It soon becomes apparently very tame and will take insects from the fingers of its captor.

Observations of Color Changes in the Living Anolis

A general fact impresses itself after one has captured and observed many of these lizards in captivity, namely, that the range of variation in the color of the skin is by far greater in those animals which have been freshly captured. After a few weeks of captivity, although seemingly in perfect health, the color changes become less complicated and less brilliant. This observation may tend to explain the differences noted by different observers as to the color changes. Ditmars states that the color varies from different shades of brown to emerald green and that although these are the common hues of Anolis, other hues are striking, namely, golden yellow and slaty gray with the peppering of white spots over the back. These colors he believes occur during the transition from the two extremes, namely, brown and green. Carlton states that he has never seen any changes other than the different shades of brown to emerald green and bases his assumption that the color changes are much more simple in Anolis than in the true chameleon, on the observations of Lockwood.

To those observing these lizards in their natural environment, it is evident that the variation is not so simple as has just been noted. A slaty gray with no element of brown or green is of fairly common occurrence, as is also straw yellow.

Furthermore over certain areas of the body the colors undergo even a greater variation than is ascribed to them by Ditmars. Over the mid-dorsal region, for instance, there is present in many of these lizards a narrow stripe of two or three millimeters in width, extending from the cervical region to the sacrum or even along the tail for a variable distance, in which further variations may be noted. That this stripe varies in different individuals is probable, and it may even be absent. Nevertheless, it is so characteristic of many specimens that a description of its changes should not be neglected. A bright pink color is often present along the stripe which may become darker until it assumes a brick-red color conveying the impression that there is placed there a thick pigment which does not belong to the skin. This stripe may also show a cream color or white, containing a faint suggestion of yellow or brown. This light color is most often observed in those lizards which have assumed the brown hue elsewhere on the body.

When the mid-dorsal stripe assumes either a pink or a white stripe it is irregular at the edges and these irregular edges are dark brown. A less irregular, black stripe is often observed in the green state.

I have been unable to discover any rule for the appearance of the dorsal stripe in its various states. It may be present or absent, brick-red, pink, white, or black in different lizards living under the same conditions, nor does the color state of the rest of the body influence the appearance to any extent. I believe that this stripe may appear at some time in all the animals in which it is absent, but that its appearance entails considerable change in the structure of the skin so that its production must necessarily be a slow one.

On the sides of the maxilla, posterior to the eye there may be present a black, quadrangular patch, measuring in large males about two by three millimeters. When present, this patch is of shiny black appearance and differs markedly from the rest of the body even in the dark brown state. This patch appears during the time when two males are preparing for combat and is associated with the appearance of the mid-dorsal ridge, the lateral flattening of the abdomen and thorax, the extension of the legs so that the body is raised off the ground, and by a peculiar greenish mottling of the skin. The altered appearance of this animal preparing for combat, in color, form and action, shows such marked changes, that it is difficult to associate it with the animal under ordinary conditions. Even the eyes, which ordinarily are fairly prominent, recede so that the palpebral fissures show only the pupils. The movements are slow and awkward and the body may sway from side to side in a most fantastic manner.

In general, the peppering of white spots on the dorso-lateral aspect of the body is characteristic, especially during the brown state, and these spots may be confluent on the lateral aspect of the cervical region. The lower border of the maxilla, the entire mandible, and the ventral aspect of the entire body varies from a snowy white to dirty brown, gray, or peppered with black dots. The throat-fan when extended is a brilliant pink or vermilion and over it are scattered many white spots. When relaxed, the skin of the throat region is somewhat cream colored or white with reddish streaks at times.

The following table indicates the various colors noted in different specimens at the same time and in the same specimen at different times:

Table Showing Range of Colors in Various Areas of the Body

I Dorso-lateral aspect:

- A Diffuse:—
  - *a.* Golden yellow to straw yellow.
  - *b.* Emerald green to dirty bluish green.
  - *c.* Slaty gray of various shades.
  - *d.* Light brown to dark mahogany brown.
- B Mottled:—
  - *a.* Yellow with irregular patches of green.
  - *b.* Yellow with irregular patches of brown.
  - *c.* Emerald green or pea green with irregular areas of darker green to brown.
  - *d.* Green or brown (usually the latter) peppered with white or light turquoise blue spots.

II Mid-dorsal stripe:
- *a.* Pink with irregular brownish border.
- *b.* Brick-red with irregular brownish border.
- *c.* White or cream color with irregular brownish border.
- *d.* Black with fairly regular border.
- *e.* Brown or green matching surrounding skin.

III Post-orbital patch:
- *a.* Black.
- *b.* Various shades matching the rest of the body.

IV Ventral surface of the body:
- *a.* White.
- *b.* White with scattered black spots.
- *c.* Dirty brown or gray.

On comparing this table with that of Brücke for *Chamæleon vulgaris*, one notices certain differences. For instance, pale flesh colors, lilac gray, steel blue and purple are not present in Anolis, but the greater simplicity which Carlton would attribute to the latter is questionable. Undoubtedly differences exist but the changes must be just as complicated in one as in the other.

Causes of Color Changes

The most evident general factors influencing the color states are light, absence of light, temperature, and various external stimuli.

Carlton found that with few exceptions the brown state was brought about from the green state in four minutes by exposure to sunlight. Absence of light changed the brown to green in twenty-five minutes. With specially constructed containers, he found that, with few exceptions, if part of the body of a green lizard, either head or body, be exposed to direct sunlight, while the rest remained in the dark, the entire body became brown.

Carlton concludes that there are nerve terminals in the skin which are directly sensitive to light and which, when stimulated in one area, send impulses which reach the efferent nerve endings of the skin over the entire body. Spinal cord section in no way changed the results, indicating that the action is either wholly reflex in character, or that spinal nerves do not necessarily influence the changes. Carlton was able to induce the green state by injections of .001% nicotin solution in small quantities and this change from brown to green was brought about in one minute. This suggested to him that this change is under the control of the sympathetic nerves.

He also found that the green state could be produced in three ways, namely, by subjecting the animals to the absence of light, by inhibiting the blood circulation, and by cutting off the nerve supply.

Inhibiting the circulation, he found, was a more important factor than cutting off the nerve supply, in that it brought about more rapidly the green state and, furthermore, when both factors acted simultaneously, still greater rapidity in change occurred than when either one acted alone.

Carlton believes that the green state represents the unstimulated state of the skin, which is suggested by the fact that ether narcosis, nicotin poisoning, and death are associated with the green state. The brown state, he believes, is brought about by stimulation of the nerve endings and represents "the state maintained through tonus established by the sympathetic nerves and dependent upon stimulation of the nervous end organs in the skin by light."

Parker and Starratt, repeating Carlton's experiments on the rapidity of change from one color state to another, obtained results that were not uniform and found that changes would occur more rapidly on one day than on another and even at different times during the same day.

By means of a constant temperature apparatus which could be illuminated at 115 candle-meters and at the same time brought from 10°C. to 50°C., they found the average length of time at various temperatures at which either the brown or green state could be produced from the opposite color state. They found that at 10°C., the skin remained brown in either light or dark, but as the temperature was raised to 20°C., the animals placed in the dark became green in 19.66 minutes. At 25°C., under the same conditions, the change took place in 13.23 minutes; at 30°C., it took 10.93 minutes; at 35°C., 15.48 minutes. At 40°C. to 45°C., the skin remained greenish gray to green in both light and darkness.

On the other hand, when green lizards were placed in the light at 20°C., the brown state was brought about in 4.23 minutes; at 25°C., 3.52 minutes; at 30°C., 3.13 minutes, and at 35°C., 2.8 minutes.

These investigators believe that at intermediate temperatures, namely, between 20°C. and 35°C., light is the controlling factor but that temperature is effective over this range is evident in that it may influence the rate of change.

Parker, in experimenting with *Phrynosoma regale*, found that the claw-like scales which fringe the lateral edge of the body became white when the animal was subjected to a temperature of 32°C. and placed in the dark, and when placed in the light these claw-like scales became almost black. At 19°C., these scales became black in 15 minutes when the animal was placed in the light, and they became white in 30 minutes in the dark. At 15°C. light again caused black, while darkness brought about a light color, but not white. From these results he concluded that a low temperature favored the production of the black state, whereas a higher temperature, the white state. Thus light produces in this animal, as in Anolis, a dark state, while its absence brings about the light state.

Parker further believes that even in Stellio, Uromastix, and Veranus, which have always been considered to have a reversal of the light reaction, in that light causes just the reverse effect as in Anolis, namely, the production of light coloration in the light and dark coloration in the dark, that the apparent reversal is really a temperature effect and not a true reversal of the effect of light.

Parker and Starratt mention the observations of Doctor Caswell Graves who stated that in the neighborhood of Beaufort, N. C., on hot, sunny days about as many green lizards as brown ones may be captured. These results are explained by Parker and Starratt by considering that some of the animals are more sensitive to light than to heat and thus become brown, while others are more sensitive to heat than to light and become green.

I do not believe that this explanation suffices, for if one notices individual lizards for a considerable length of time, one is struck by the frequent and rapid changes from green to brown and back again to green, apparently regardless of temperature and light. How much influence the otherwise varying nervous conditions exert on these color changes, it is difficult to say for it would seem almost impossible to control them. I have watched animals which were sunning themselves and apparently undisturbed and quiet undergo these changes in a rhythmic manner. Rapid changes are also frequently noticed when an Anolis changes slowly from one object to another, the change occurring while the transfer is being made.

Redfield, after numerous carefully checked experiments on *Phrynosoma cornutum*, was able to verify the conclusions of Parker, Carlton, Starratt, and others that the daily rhythmic changes of color are produced by the direct action of light and heat upon the melanaphores. He further states that Phrynosoma adapts itself to its surroundings, namely, if placed on a substratum of white sand it slowly assumes a light coloration irrespective of light or heat and if placed on a substratum of cinders it slowly takes on a dark coloration. He concludes that the color adaptation depends upon stimuli received through the eyes.

He was able to bring about a pale coloration in various ways, such as forcibly opening the mouth or by the application of a weak faradic current to the mucous membranes of the mouth or cloaca. He believes that this proximal migration of the pigment may be brought about in two ways, namely, by nervous impulses which stimulate the melanophores through the sympathetic nervous system or by secretion of a hormone (adrenin) from the adrenals. The impulses are carried from the mouth or cloaca along the spinal cord to a center situated between eighth and thirteenth vertebræ and thence by sympathetic fibres to the adrenals. The stimulated glands secrete adrenin which is taken up by the blood stream and acts directly on the melanophores causing a proximal migration of the pigment.

Redfield concludes from the fact that adrenalin produces proximal migration of the pigment in Anolis and from the work of Carlton, that impulses through the autonomic nervous system cause a distal migration of the pigment, that the melanophores of Anolis must possess a double innervation from two divisions of the autonomic nervous system. That this is possible he shows by analogous tissue, namely, the smooth muscle, the latter one "known to be innervated by antagonistic fibres belonging to two morphologically distinct parts of the autonomic nervous system."

The explanation for emotional manifestations in Phrynosoma, Anolis and other animals is readily explained by his conclusions regarding the secretion of adrenin.

When first placed in captivity the brown and green lizards in the same cage are about equally divided, but after remaining in captivity for a few weeks the greater proportion become brown in the daylight and the green produced by the absence of light has lost its former brilliance.

Much has been written about the true chameleon and its adaptation of color to its surroundings. Keller found, after placing specimens of *Chamæleon vulgaris* in a green house, that in a short space of time he was able to find them only after a most careful search, in spite of the fact that when found they were often in plain view. However, he does not believe that the surrounding color plays any role but that other factors, which he did not attempt to explain, bring about these changes. Ditmars states that there is no relation between the color of Anolis and its surroundings.

One must have great temerity to deny such a statement, but I have noted adaptations to the surroundings in Anolis which seem to be more than accidental. For instance, I have noticed that on dark brown fence rails which contained small areas of green lichen, some of the lizards resting on them assume a dark brown color with irregular patches of brilliant green. In other words, a mixed state is often evident and the effect produced resembles fairly closely the surroundings. Almost invariably the lizards seen on the trunks of the palm trees in New Orleans are brown and are often detected with great difficulty.

The table below represents the findings on May 16, 1917, from 11.30 A. M. to 1.45 P. M., during which time the temperature was 25.5°C. The environment is stated, as well as the number of lizards noted thereon, and the intensity of their color state. G represents green and B brown. The sign +++ represents the greatest intensity of either green or brown, namely, either emerald green or mahogany brown, ++ represents a less intense color but still quite marked, while + indicates the least degree of intensity but one in which one is able to definitely state the color as being either green or brown.

TABLE 2

	Number of green lizards			
	G +++	G ++	G +	Total G
Green foliage	0	2	6	8
Dark green foliage	1	0	1	2
Concrete	2	0	1	3
Brown tree trunk	0	0	2	2
Fence rail	2	3	6	11
Totals	5	5	16	26

	Number of brown lizards				
	B +++	B ++	B +	Total B	Total G & B
Green foliage	0	0	0	0	8
Dark green foliage	1	1	0	2	4
Concrete	1	2	0	3	6
Brown tree trunk	0	1	0	1	3
Fence rail	1	3	7	11	22
Totals	3	7	7	17	43

Except the lizards seen on green foliage, the number of green animals equals the brown ones. No brown ones were noted on green foliage but the observations here recorded are by far too limited to permit definite conclusions to be drawn. There was some difficulty in deciding whether an animal resting on a brown fence rail amid a mass of green foliage should be classed as one resting on a fence rail or on green foliage, but it was decided to place these with the former.

One is justified, however, in drawing one conclusion from the table, namely, that under approximately the same conditions of temperature and light both green and brown lizards may be found and, even on sunshiny days with a moderate temperature, the green ones may even outnumber the brown ones. According to Parker, brown should be the prevailing color. It does not appear that in their natural environment the reason for the greater number of green lizards can be accounted for on the ground that these animals reacted more strongly to temperature than to light.

According to Parker and Starratt, the Anolis remains brown at 10°C. and remains green at 40°C., regardless of light. One would expect then, that at a temperature of 25.5°C., if there were a greater susceptibility to temperature, the brown state would prevail for at this temperature there is active both the light and medium temperature influence.

Evidently a factor which is of extreme importance in influencing the color state is the emotional or nervous condition which can not be easily controlled. The effect of the organs of internal secretion which are under the control, directly or indirectly, of the nervous system probably also influences the color states.

Ditmars states that the sleeping Anolis is invariably green and that the same color is present during anger or fear. He states that if a cage containing a number of these lizards be shaken, all take on the green state, but after allowing them to rest for a short time, most of them assume the brown state. I have found this to be true in general. Also, if a brown Anolis is taken out of its cage and held in the hand it becomes green in a few minutes. This characteristic change occurs quickly even in animals which have been kept in captivity for a number of weeks and have apparently become tame.

It is evident that various factors influence color states and the problem becomes even more complex when one considers that certain areas of the skin may be light colored, as in the case of the mid-dorsal stripe, while the rest of the skin may be dark. One must admit that the skin is influenced by three factors, temperature, light and emotional or nervous conditions, induced, no doubt, by way of sense organ stimuli. Yet we get opposite effects in two areas of the skin of the same animal. One would hardly expect light and temperature to have a selective action on the skin.

Structure of the Skin of Anolis

The chief object of this paper is to present a review of the histological structure of the skin of Anolis and to add some observations with the hope that the further investigation of the color changes may be enhanced and some of the factors governing the color states explained. It is not claimed that a knowledge of the minute structures and their relations will offer a full explanation of these changes, but without such a knowledge, physiological experiments must fail to accomplish this end. It is only by keeping in mind the structure of the skin that the actual processes involved may be surmized and physiological data be applied in actual explanation of the problems.

The skin of Anolis is comparatively thin and loosely attached except at the sides and dorsum of the head and tail. On closer observation it is seen that it is not smooth but is thickly studded with small, closely-packed scales which vary in shape, color, and size in different parts of the body. These small scales, designated as *scutes* by Carlton, are smooth and shiny.

The scales situated along the mid-dorsal line are irregular in shape and size with slight tendency toward a hexagonal outline (Fig. 1). They are well separated and measure 0.29 mm. lengthwise to the body and 0.305 mm. in the transverse direction. A thickened, linear, longitudinal keel may be present in the mid-line of the scale. The scales on the dorso-lateral aspect of the body are less irregular than those along the mid-dorsal line and none shows overlapping. They measure 0.248 mm. x 0.265 mm. (Fig. 2). Those scales on the lateral aspect of the body are almost circular in outline and are arranged in two rows, vertical and horizontal, the intersection of the two rows making an angle of about 58°, and they measure 0.255 mm. x 0.248 mm. (Fig. 3).

The scales on the ventral aspect are larger and more closely arranged, the caudal edge of each scale overlapping slightly the cephalic end of the scale just behind it. The outline of the scale is somewhat oval or circular and there is present a horny ridge or keel extending down the middle which becomes more prominent as the caudal border is approached. The scales of the region measure 0.35 mm. x 0.36 mm. (Fig. 4).

The scales on the tail differ markedly from those previously described. They are hexagonal in outline and closely packed and overlap each other to a greater extent than those on the ventral surface. There is present a median ridge and the surfaces on either side slope away from it. These scales measure 0.45 mm. x 0.27 mm. (Fig. 5).

The dorsal aspect of the head is made up of bilaterally symmetrical plates of a more or less hexagonal form. Just posterior to the intersection of the mid-dorsal line and the posterior edge of the orbital ridge is a marked pineal eye. The scales on the distended throat-fan are widely separated and are flattened and somewhat conical in shape. Those of the eyelids are so minute as to be barely visible.

The color of the individual scales is the same as that described for the various areas of the body. When a general color state is assumed, for instance brown, isolated scales may be white, turquoise blue, lighter or darker brown than the general hue, or even green.

Some extremely interesting features are noted in scales on the various parts of the body when observed under the low power of the microscope, by reflected and by transmitted light. The characteristics exhibited by the scales present points of similarity, but also some very marked differences. For these observations bits of fresh skin were taken from different parts of the body and mounted in glycerin and the appearance of the scales was studied both from the external surface and from the internal surface.

The external surface of the lateral scales appears yellow by transmitted light. Scattered evenly throughout are somewhat indistinct, pale brown, stellate-shaped bodies, the melanophores, which average about fifty in number for each scale. The spaces between the scales are transparent and contain many branching pigment cells (Fig. 6 A). By reflected light these scales appear emerald green and the interspaces black (Fig. 6 B). The internal surface appears blue by reflected light and the branching melanophores appear distinct and dark brown or black (Fig. 6 C).

The external surface of the scales of the ventral surface appears a pale straw color by transmitted light and contains isolated indistinct pale brown melanophores of from four to twelve in number. The branches of these melanophores become darker near their termination (Fig. 7 A). By reflected light the scales appear somewhat as inverted glass cups containing crushed ice and the melanophores are cobalt blue except at the termination of their branches which are brown (Fig. 7 B). The internal surface by transmitted light appears a pale straw color and the melanophores are distinct and black (Fig. 7 C).

The scales along the mid-dorsal stripe differ from those just described in that, irrespective of other colors, they have a peculiar pinkish cast while the melanophores are much fewer in number in many scales and lighter in color than those previously described.

The scales of the throat-fan are pale straw color by reflected light and show the blue appearing melanophores. The wide spaces between the scales present many bright red linear streaks of varying sizes which branch and anastomose. The underlying color is pink and of granular appearance. By transmitted light the melanophores appear brown and more distinct and the spaces between the scales take on an orange color. Injections of india ink into the circulation would tend to show that the pink color is not entirely due to the vascularity of this structure but to some other coloring matter present.

It would appear from the differences noted by reflected and transmitted light that the melanophores are separated from the surface of the scale by some substance which gives them a bluish cast by reflected light and pale brown by transmitted light. That they themselves are black is evident by viewing them from the internal surface of the scale where they present a sharp clear outline (Fig. 6 A, B and C). In order to explain the green color of the scales of the lateral aspect of the body it is necessary to eliminate the yellow coloring matter which is noted by transmitted light. This may easily be accomplished by subjecting the skin to alcohol and ether in which this yellow substance readily dissolves. When the scales are now viewed externally by reflected light, they no longer have the green appearance, but appear deep blue just as do the previously described scales viewed from the internal surface by reflected light (Fig. 6 C). The melanophores, however, are blue and indistinct, indicating, as was later found, that a semi-transparent reflecting layer exists between them and the surface and that this layer is evidently not affected by ether or alcohol.

The explanation for the green color is now quite apparent, for blue rays are reflected and these in passing through a clear yellow medium present to the eye the green color.

The semi-transparent reflecting layer lying between the melanophores and the external surface reflects bluish-white light as is evident in those scales in which little or no coloring matter exists and in which the melanophores are sufficiently separated so as not to influence the reflected light to any extent. This is true of the scales on the ventral aspect of the body, in individual lateral scales, and the white ones often found along the mid-dorsal line.

Histology

That the tissue relationship of the skin might be more carefully analyzed with the purpose of attempting an explanation for the changes of color, a number of lizards in various color states were killed and segments of the body fixed in different fluids. It was found that segments placed for about six weeks in a fluid consisting of 3.5% potassium bichromate 100 parts, formalin 4 parts, and glacial acetic acid 5 parts, gave the best results. Tissue fixed in this fluid maintained the cellular relationship and the osseous structures were sufficiently decalcified so that entire sections of the body could be made.

Formalin was found to act too slowly with segments of the body. Lizards in the green state became brown during its action. It was possible, however, to overcome this difficulty by injecting formalin quickly with a hypodermic needle under the green skin, thus obtaining almost immediate contact of the fluid with the entire internal surface of the skin. This method has a distinct advantage in that the animals may be studied on the table for a considerable length of time after fixation and the color state carefully recorded. Unfortunately, however, after a longer time the green color becomes changed to a slaty gray after the use of formalin, due most probably to a change in the yellow coloring matter. Removing the skin and washing it in water soon after fixing prevents this bleaching and bits of skin may then be held between pieces of hardened celloidin and sectioned. The solubility of the yellow substance forbids imbedding in either celloidin or paraffin. These sections should then be mounted in glycerine.

For examination of the cellular elements, tissues imbedded in both celloidin and paraffin were sectioned at 15 microns and stained with haematoxylin and eosin. Frozen sections treated with gold chloride for the purpose of showing the nerve endings have, so far, not been successful.

In order that the histological picture be made as complete as possible, the elements of a single lateral scale will be described (Figs. 10, 11, 12, 13 and 14). Where differences exist in the scales of other parts of the skin these will be mentioned. The layers comprising the scale will be taken up in their order, beginning from without inward.

Epidermis.—The outermost, transparent layer or epidermis may be divided into an outer, horny layer or stratum corneum and an inner, stratum germinativum. The epidermis is considerably thicker near the summit of the scale than at the periphery where it becomes continuous with the thin epidermis of the space between the scales.

The stratum corneum may usually be divided into two layers, an outer one which is separated by an interspace from an inner. This outer layer represents that portion which is ready to be cast off in moulting (Figs. 8 and 12). The inner layer does not stain with eosin, being straw-colored. The squamous cells may show clear, non-staining, round bodies, representing the degenerated nuclei. The layer undergoes marked keratinization at the apex of the scale with the formation of a homogeneous, horny ridge or keel. This thickening is more marked in the scales on the ventral aspect and those along the mid-dorsal line. Keratinization of the other cells of the stratum corneum, other than in the keel, is not so marked and, due to the dehydrating effect of the air, become fairly well separated so that their outlines may be distinguished (Fig. 8).

Brücke has described "interference cells" in the outer layer of the stratum corneum in *Chamæleon vulgaris*. These cells, he believes, modify the color of the skin by reflected light to a very marked extent.

Keller believes that the outer cells of the outer layer of the stratum corneum contain minute closely placed columns arranged at right angles to the surface of the cell. He calls this outer layer the "Relief Schicht," and the inner surface of this outer layer the "Negative Relief Schicht." The latter presents the negative picture of the former in that instead of minute columns there are toothlike incisions corresponding to the columns of the "Relief Schicht." The layer between these two he terms the stratum corneum. He further claims that the outer cells of the inner layer of the stratum corneum are similar to those of the outer layer and terms them the "Second Relief Schicht." He believes that separation occurs along a line corresponding to the boundary between the "Negative Relief Schicht" and the second "Relief Schicht" and that when the outer layer is cast off the second "Relief Schicht" becomes the first and then a second line of cleavage occurs making a second "Relief Schicht" and a "Negative Relief Schicht." This cleavage goes on at regular intervals. He found that the fine column-like structures of the cells were very much more pronounced in the foot pads and at the apices of the scales.

In Anolis the first or outer "Relief Schicht" of Keller is very prominent on the under surface of the adhesive pads of the second phalanges. The second "Relief Schicht" is also present when the outer layer of the stratum corneum is well separated from the inner layer, but no "Negative Relief Schicht" was noted. On the outer cells of the outer layer of the stratum corneum of the scales of the general body, occasionally minute spicules resembling short cilia may be seen in stained preparations but such occurrence seemed very rare. In dried scrapings, the outer cells seen on the flat contain numerous dots giving them a stippled appearance when examined with the high dry or oil immersion lens. These probably represent the spicules that Keller has described for the chameleon. (See Fig. 9.)

The stratum germinativum takes the haematoxylin and eosin well. The cells are polygonal with fairly large vesicular nuclei. In the scales this layer is from two to three cells thick but in the epidermis between the scales it is at most only two cells thick. The basal layer is composed of cuboidal and columnar cells with large vesicular nuclei. Their proximal borders, attached to an ill-defined basement membrane, are frayed and brush-like (Fig. 8).

That the epidermis, through phenomena of interference, exerts some modifying influence on the color of the skin in Anolis is without doubt, but that it plays the important role which Brücke ascribes to it for the chameleon is doubtful. Keller, in fact, disagrees with Brücke as to the importance of this layer even in the chameleon. The small, transparent spicules in the outer layer possibly cause some diffraction of light but this must be slight for the underlying cellular outlines are markedly clear when viewed through the epidermis.

The Oil Droplet Layer.—A considerable amount of confusion exists in regard to the layer underlying the epidermis. Keller has described a layer in the chameleon which he designates the ochrophore layer. He does not believe that it is cellular for the elements composing it have no nuclei, but he believes that it is made up of bits of cytoplasm cast off from an underlying layer of cells which he terms the leucophore layer. This ochrophore layer is found on the dorso-lateral aspect of the body but is almost entirely absent on the ventral aspect and entirely so on the foot-pads and spaces between the scales. Keller found that the elements of the layer were brownish yellow by transmitted light and a bluish white by reflected light, had a granular appearance, and that they disappeared under the influence of mineral acids. He described these elements as more or less spindle shaped and vertically arranged, the ends in contact with the epidermis being more pointed than those of the opposite end. The elements farther removed from the epidermis had both ends rounded.

Pouchet called this layer "Iridocytes" and believed the elements to be cells although he could not make out the cellular structure.

In Anolis, Carlton describes what he believes to be the ochrophore layer of Keller. He admits that its structure is not similar to that found in the chameleon. I do not believe that Carlton saw a layer corresponding to that in the chameleon, but that he described the leucophore layer which he mistook for the ochrophore layer. I will take up my reasons for this assumption in the discussion of the leucophore layer.

In sections stained with haematoxylin and eosin, I was unable to make out any layer corresponding in either position, structure, or color to the ochrophore layer. In certain scales, more often those situated along the mid-dorsal line, a clear space or a space filled with large clear cells with large vesicular nuclei could be noted where the ochrophore layer should lie. Knowing that it was possible to dissolve out the yellow coloring matter in the scales with alcohol and ether, it did not seem improbable that in the preparation of the stained sections practically all trace of this layer had been lost.

For this reason formalin fixed skin was sectioned between blocks of celloidin very soon after fixing and then mounted in glycerine. In these sections, there is situated just beneath the epidermis a thin layer made up of bright yellow droplets of varying sizes (Fig. 10). These droplets appear beautifully refractive, do not contain any granular material, nor are they arranged like the elements in the ochrophore layer of Keller. Some of these droplets may even be found at times between the basal cells of the epidermis where they have probably migrated.

By transmitted light this layer of droplets appears bright yellow (Fig. 10 A), while by reflected light it disappears almost entirely, in other words it does not reflect light to any marked extent (Fig. 10 B). In this respect it differs from the ochrophore layer of Keller, which its describer found to be bluish white by reflected light.

The sections treated with Scharlach R caused this layer to become brownish red, indicating that the droplets composing it are lipochromes.

This layer of oil droplets is practically absent on the ventral surface of the body and entirely so on the adhesive pads of the feet. To what extent it is present along the mid-dorsal stripe, I am unwilling to say. That it occurs here in individual lizards to the same extent as on the lateral scales is true; but whether it is greatly diminished in those lizards showing a white dorsal stripe, or whether it is present to the same extent but can be displaced to the periphery of the scale by a special mechanism and there does not effect the color, it is difficult to say. Keller believes that this layer can be removed from the field of action by special cells.

One may conclude, then, that beneath the epidermis of the dorso-lateral scales there is a thin layer made up of transparent yellow oil droplets and that this disappears in stained preparations due to its solubility in alcohol, ether and clearing oils.

Zanthophores.—Lying just beneath the epidermis of the lateral aspect of the body and in the oil droplet layer, are cells of varying sizes. The larger cells have a clear, round, unstained cytoplasm in the sections stained with haematoxylin and eosin. The nuclei are large and vesicular and the chromatic elements stain deeply (Figs. 11 and 14). The number of these cells varies in the scales of the different parts of the body, being probably more numerous along the mid-dorsal stripe. In fresh specimens it was practically impossible to distinguish them with accuracy. These cells were not described by Carlton, but Keller has described similar cells for the chameleon and named them zanthophores, and Pouchet also described similar cells for the chameleon and believed that they contained fat droplets of 2.5 microns. He believed these cells to be analogous to the yellow cells of batrachians and that they possessed the power of contractility. Keller also believed that they could expand or contract for he found them varying markedly in size. Doctor Irving Hardesty suggests that these cells secrete or control the accumulation of the oil droplet layer described above.

If Keller and Pouchet be correct in their assumption that these large clear cells may expand, one might reason that during this state they practically fill the entire space between the epidermis and the underlying layer and force the yellow droplet layer towards the periphery of the scale so that it no longer influences the color states.

For reasons which will be taken up later, I believe that the mechanism is not quite as Keller would have one believe, although undoubtedly these cells are more numerous and almost replace the oil droplet layer in the white scales of the mid-dorsal stripe. If these large, spherical cells in Anolis are the zanthophores of Keller, and they resemble very closely those he figures and describes, Carlton is wrong in stating that these cells do not exist in Anolis.

The Leucophore or Guanophore Layer.—The layer lying just beneath the layer of oil droplets presents very marked differences from any of the structures previously described. In vertically sectioned scales, stained with haematoxylin and eosin, it is seen that this layer is thicker near the center of the scale and then gradually thins out until it disappears at the periphery. The layer forms then an inverted cup which thins out at the edges and fits into the hollow epidermal scale but does not come in immediate contact with it because of the intervening oil droplet layer. It is present in all the scales of the skin including those of the ventral aspect of the body (Figs. 8, 10, 11, 12, 13, 14 and 17). By reflected light it appears as a homogeneous bluish-white band (Fig. 10 B), and this appearance is not lost in those sections fixed in the fluid mentioned and stained with haematoxylin and eosin. Bits of the layer may be found isolated in the deeper fibrous layer, recognizable by the bluish-white color.

By allowing a minimal amount of light to come through the condenser of the microscope, the layer has a most brilliant opalescent appearance. In unstained, freshly fixed formalin sections, by transmitted light, it has a pale brownish appearance (Fig. 10 A), but in stained sections it appears darker and greenish brown (Figs. 11, 12, 13 and 14).

Fig. 10, A and B, represents the appearance of an unstained section of the layer by reflected and transmitted light. By reflected light this layer appears as a bluish-white cloud which obliterates the underlying structures, or at least makes them appear hazy and indistinct.

In both the stained and unstained vertical sections the layer is seen to be composed of parallel rows of somewhat irregular blocks, their long axes being parallel to the outline of the epidermis. These blocks are of varying size and asymmetrical shape, and undoubtedly possess small, deeply staining nuclei. Some sections show these nuclei better than others. The vertical section gives little idea of their morphology for when seen in tangentially cut sections they appear very irregular in outline and possess short pseudopodoid processes which may terminate in hooklike expansions or branches. Every conceivable shape exists and no similarity exists in these bodies except in their marked irregularity (Fig 14). In some sections these cells appear syncytial, for their processes are in juxtaposition, thus leaving numerous openings of various sizes between these apparently joined processes. Through these openings run the branches of the melanophores (Figs. 14 and 17). That really no syncytium exists appears likely, for in vertical sections no such connections between the processes can be made out. When viewed from above, the area around the nucleus has a bluish cast while the periphery is a pale greenish brown.

One can conclude then that the cells of this layer are fairly thick, irregular plates of fairly uniform thickness throughout but with a marked irregular outline.

Carlton describes a somewhat similar layer in the scale of Anolis which he calls the ochrophore layer and which he considers analogous to the ochrophore layer of Keller for the chameleon. He believes that this layer produces the green color and finds that by reflected light it appears bluish green and by transmitted light yellowish green. From the micro-photographs accompanying his paper, one cannot be mistaken as to the identity of the layer in question. He has noted the block-like, parallel arrangement in the vertical section and also the irregular appearance in the tangential section, stating that it had the appearance of a more or less homogeneous mass, irregular in outline, and penetrated in many places by the processes of the melenophores but he was unable to make out any cellular structure and denied the existence of nuclei except between the blocks. Why he should believe this layer to be the ochrophore layer of Keller, I am unable to say. He admits that its arrangement differs from Keller's ochrophore layer.

If Carlton's ochrophore layer is responsible for the green state in Anolis, why is this layer present on the ventral aspect of the animal where no green color is ever present?

Keller states that this ochrophore layer is almost entirely absent on the ventral aspect of the body of the chameleon, yet Carlton, in spite of these differences in structure and position, attempts to make these two layers analogous. Furthermore, Carlton's ochrophore layer closely fits the description of Keller's leucophore layer, which latter Carlton states does not exist in Anolis.

Undoubtedly the layer in Anolis is the same as that in the chameleon except for possibly minor differences.

Brücke described in the chameleon a white or yellow pigment which he finds separated into two layers, the inner being thicker and made up of closely packed colorless particles with rounded boundaries, which reflect light, resulting in the white appearance. He believes these reflecting granules to be the product of cells whose processes force themselves between the dermal structures and lie between the epidermis and the underlying connective tissue. In these two layers he evidently includes both the ochrophore layer and the leucophore layer of Keller.

Pouchet has also described this layer and considers the white, dust-like material as the products of cells which, by the growth of the neighboring tissue, have been pressed into plates, and Keller describes these plates or blocks which he names leucophores. He considers their content similar to that found in the scales of certain fish described by Kühne and which are said to be composed of guanine. The fact that both react positively to the murexide test leads to this assumption. He believes, as does Pouchet, that these leucophores have been pressed into plates by the pressure of the overlying and underlying tissues and that their edges adapt themselves to the neighboring structures due to the mechanical resistance of the latter, and, in consequence, assume very irregular shapes except in those regions where no such pressure is exerted. In regions where no pressure is exerted, they are rounded and lie close together in the wide meshes of the connective tissue.

I was unable to verify Keller's observations that the leucophores were rounded in those regions where the mechanical resistance is less, for those isolated cells which were noted by me showed in reality even greater irregularity, when seen in vertical section, than those in the leucophore layer proper. That the peculiar plate or block-like shape and the arrangement of these in parallel rows may be due to the pressure of the dense connective tissue from below seems likely, but only careful observations of the skin in various stages of development can determine this point.

The white, dust-like material of Pouchet, the white pigment of Brücke, or the granules of Keller, which were described in the leucophores, were not noted by me in Anolis. The cytoplasm of these cells even in the fresh state was clear and apparently free from granules. This finding is interesting in that one would expect the reflecting power of these cells to be due to the denser granules, and probably such granules do exist but were invisible because of methods I employed in the study of these cells.

No differences in shape or position were noted in the leucophore layer in the green and brown state. The cells of the layer seem to retain their characteristic appearance and relationship no matter what color state of the skin existed. Carlton makes the same observation for his so-called ochrophore layer.

The blue coloration of the melanophores by reflected light described for the scales of the ventral aspect of the body is undoubtedly due to the leucophore layer as is also the white appearance of these scales. This will be touched upon later.

The Melanophores.—Lying between the leucophore layer and the underlying connective tissue layer, and partially imbedded in both, are the melanophores described by Keller for the chameleon (Figs. 10, 11, 12, 13, 14, 15, 16, 17).

In Anolis three types of pigment cells are found, namely, those in the dorso-lateral scales which differ from those in the ventral scales by their smaller size and more delicate branching, those in the ventral scales, and a third type which is commonly situated just beneath the epidermis between the scales. The melanophores show a striking resemblance to the Purkinje cells as seen in Golgi preparations. A line passing through the cell bodies of the majority of them would be more or less parallel to the epidermis except at the periphery of the scale where they more closely approach the surface. A few cell bodies lie above or below this imaginary line, but in thick sections the bodies of the melanophores form a fairly thick, dark-brown layer of fairly regular width.

The melanophores are best studied in vertical sections of the fixed material stained with haematoxylin and eosin. It was found unnecessary to use the methods adopted by Keller and others to bring out the finer branches of these cells, for in most of the preparations these were clearly visible.

The cell body is more or less rounded but considerable difference exists among them, some being much narrower than others (Figs. 11 and 12). The surface facing the epidermis is often concave but rarely it may be convex or apical. The nucleus may be round, oval, reniform, horseshoe-shaped or even double in rare instances. In some preparations it takes a fairly deep blue stain and has a vesicular appearance (Figs. 11, 15 and 17). The concavity when present is directed towards the epidermis.

Coming off from the sides of the outer surface of the cell body are a varying number of permanent branches which run either vertically toward the inner surface of the epidermis or present a lateral curvature. The curvature may even be so marked that, at the proximal part, the branches may be directed first downwards and laterally and then gradually curve laterally and upwards (Figs. 11, 12, 13 and 15). These branches run through the spaces among the leucophores and, as they approach the surface, lateral branches in turn give off further branches. This tree-like branching continues until beneath the under surface of the epidermis a layer of fine terminal branches exists.

The contents of the melanophores consists of a varying amount of fine pigment granules imbedded in a mass of faintly brown, poorly staining cytoplasm. The arrangement and distribution of the pigment granules depends on the color state of the skin, being almost absent in the smaller branches in the green state but present even in the terminal branches in the brown state. Under the oil immersion lens the poorly staining cytoplasm may be followed even in the finest branches lying beneath the epidermis. Following them is, however, greatly facilitated by the presence of isolated pigment granules which have failed to migrate with the general mass of pigment.

The pigment granules are oval in shape and brown under magnification. Their number varies markedly, irrespective of the distribution of the pigment. The number varies not only in melanophores in the same scale, but also melanophores of one scale may contain more pigment than those of another. Also the intensity of the color of the pigment may vary, individual or groups of melanophores containing a lighter brown pigment than others. This appears to be irrespective of the number of granules. These differences in amount and intensity in color are so striking that there is no doubt as to their occurrence (Figs. 11, 12 and 13).

In the green state of the skin of Anolis (Figs. 10 and 11) the pigment granules are present only in the bodies and proximal parts of the primary branches of the melanophores. This proximal migration of the pigment is practically complete and the finer distal branches are clear and transparent. In some of these finer branches, however, a few scattered pigment granules may have failed to follow the mass of pigment and their presence allows one to detect more readily the finer branches. The bodies of the melanophores during the proximal migration of the pigment are necessarily darker than after distal migration. In proximal migration of the pigment it is noticed in the primary branches of the melanophores that there is an area of gradation between the dense pigment on one side and the clear part on the other side where the pigment is much less dense. In this portion the pigment granules apparently arrange themselves in parallel rows (Figs. 11 and 15). This parallel arrangement has also been observed by Keller in the chameleon.

In the brown state (Figs. 12 and 13) the finest branches lying immediately beneath the epidermis are filled with closely packed pigment. This gives the appearance of a thin, dark-brown layer lying just beneath the epidermis in vertical section. One might conclude that, in order that this appearance can be produced, the terminal branches must anastomose and form a plexus. That this is not the case, however, may be readily determined in tangentially cut sections where the terminal branches appear as separated but closely packed, dark-brown dots (Fig. 14). Keller makes this observation for the chameleon and Carlton for Anolis.

It is probable that the green state of Anolis does not represent the maximum degree of proximal migration of the pigment. In certain scales, pigment may be absent even in the primary branches and be confined entirely to the cell body which appears like a dark brown or black sphere. Furthermore the pigment may be condensed to such a degree that a clear broad halo of cytoplasm may surround a central compacted mass of pigment (Fig. 15 A and B). These peculiar melanophores are often bilaterally arranged and present in a group of from two to three scales on each side of the body. This bilateral arrangement appears too marked to be accidental. Melanophores in this condition must explain the yellow colors and white scales often to be observed in the living Anolis.

Besides the distal and proximal migration of the pigment, any degree of migration may be present, namely, all but the terminal branches may be filled with pigment, or the terminal branches may contain scattered pigment, and so on. All of these conditions influence the color state of the skin and must be associated with definite color states.

The number of melanophores varies considerably in the various scales, but the average for those of the lateral aspect of the body is about fifty in number. This number is greatly reduced in the scales along the mid-dorsal line which are white and in which ten to fifteen pale brown melanophores appear to be the usual number. The latter are slightly smaller and their branches are more delicate and spread out more than the others. In the mid-dorsal line of other specimens where no white stripe exists but where color changes resemble those of the lateral aspect of the body, the melanophores cannot be distinguished from the others and appear in about the same number.

The melanophores in the scales, on the ventral aspect of the body are from five to twelve in number. Their bodies are larger and more rounded and possess fewer primary branches. The terminal branches are followed with greater difficulty to the periphery. The pigment is usually thickly packed in the cell bodies giving the cells a dark-brown color. The nucleus due to this increased amount of pigment is rarely observed (Fig. 8).

The pigment cells lying in the spaces between the scales vary markedly in number and position and, aside from their possession of branches and pigment content, show little resemblance to the true melanophores (Figs. 11, 12, 13 and 16). They more nearly resemble ordinary mesenchymal pigment corpuscles. The body resembles a flattened disc as is readily seen by comparing the vertical diameter as seen in vertical section (Fig. 13) with the horizontal diameter as seen from above (Fig. 16). The primary branches are thick and irregular and vary considerably in length. The terminal branches are short and terminate broadly in club-like ends. The cells are present just beneath the epidermis between the scales, their branches spreading out and lying parallel to it. These cells may often be found in the deeper tissues of the body and give the impression of their being able to wander between the tissues (Fig. 13). That these cells may be converted into melanophores seems possible.

That the pigment granules migrate in the fixed pseudopodic processes of the melanophores, instead of an amœboid extension of and retraction of the processes themselves, is very probable. This migration has been clearly illustrated by Keller and Brücke for the chameleon, Carlton for Anolis, Degner for *Praunus flexuosus*, Kahn and Lieben for *Rana temporaria* and Spaeth for *Fundulus heteroclitus*. Parker believes that the pigment migration is true for Phyrnosoma and, further, states that the migration of pigment in melanophores is influenced by light and temperature, either light or low temperature causing a distal migration and absence of light or high temperature causing a proximal migration.

Although fully agreeing that the melanophores and their processes remain fixed and that their pigment undergoes migration, I am unable to see how any set of factors influence all melanophores similarly. Under precisely similar conditions the melanophores of the lateral aspect of the body may contain proximally migrated pigment, whereas the melanophores of the mid-dorsal stripe or melanophores of isolated scales may have the pigment in the terminal branches. In a single animal, in any color state, many exceptions may be found to the rule laid down by Parker.

Gold chloride preparations repeatedly fail to reveal any nerve endings terminating on the bodies of the melanophores but that these exist seems most probable. Pouchet described a smaller pigment-bearing cell which he termed the erythrophore and which closely resembled the melanophore except that it contained a purplish-red pigment. Brücke overlooked these cells of Pouchet, but according to Keller, the cells only occur on the lateral scales of the chameleon in any great number and are not present in all individuals. Keller described gradation forms, cells containing both brown and red granules in different proportions. Some cells may contain only a few red granules among brown ones while others may contain only a few brown ones, the greater proportion being red.

Carlton was unable to find erythrophores in the skin of Anolis and denied their existence. I believe that Carlton is correct, for if these cells be present they must be extremely rare. No red pigment granules were observed in any melanophores of my sections.

It seems likely, however, that the pigment granules vary considerably in the intensity of their color as has already been stated. This conclusion is reached not only from a study of the pigment granules in the melanophores but also from their effect on the color of the skin. There is little doubt that a condensed mass of pigment will produce a darker brown than more scattered pigment, but the former will always be brown and can never be black or brick-red.

If this be true, then the melanophores producing the post-orbital black patch must contain black pigment granules and those producing the brick-red stripe must contain reddish-brown granules. Furthermore, it is possible that an individual scale may contain melanophores of two or more kinds of pigment content and that these may act independently of one another. This is suggested by the microscopic appearance as well as the appearance of either a brick-red, brown, or black state in the scales of the mid-dorsal and the post-orbital stripes. Undoubtedly the amount of pigment present plays an important role, but many of these differences cannot be satisfactorily explained. Partial distal migration may be responsible for a lighter brown color than maximal distal migration, but only up to a certain point. Any distal migration beyond this is not associated with a still lighter brown state but with a slaty or greenish-gray color.

The Connective Tissue Layer.—Lying beneath the leucophore layer, running into the concavity of the scale for a variable distance but approaching more closely the epidermis at the edges of the scale, is a fairly dense layer of white, fibrous connective tissue (Figs. 8, 10, 11, 12 and 13). The fibres appear to run parallel but on closer inspection many vertical and oblique ones may be noted. The vertical fibres may be traced as they ascend among the cells of the leucophore layer where they break up into small fibril bundles which form a network beneath the epidermis. This layer takes on a bright pink color with eosin and contains many deeply staining stellate and spindle shaped nuclei. It is fairly vascular and nerves may be seen traversing it. Below the concavity of the scale are present fat corpuscles and large blood vessels (Figs. 11, 12 and 13). Beneath the dense connective tissue separating the skin from the underlying skeletal muscles, there is present a loose areolar connective tissue. Fine free pigment granules forming a fine line between the denser connective tissue and the looser areolar tissue, may be seen in many sections. Free granules of red color aid in giving the red color to the extended throat-fan.

The skin is extremely vascular but more so in some regions than in others. Larger vessels run beneath the denser connective tissue layer and run parallel with it, dipping into the scale. From these vessels branches are given off which run through the denser connective tissue and also through the leucophore layer to directly supply the epidermis (Fig. 13). It seems not improbable that a vaso-dilatation occurring under and in the leucophore layer, may exert a modifying influence on the color states. The pink color of the mid-dorsal stripe may be explained by the effect of a vaso-dilatation on a white stripe, and the red appearance of the throat-fan is no doubt in part due to blood, as well as to granules of red pigment in the subcutaneous connective tissue, which shows through the spaces between the scales.

On the Mechanism of the Color Changes

The essential structures present for the production of the various color states are the epidermis, the yellow oil droplet layer, the leucophore layer, the melanophores, and, possibly, the zanthophores and the cutaneous blood supply.

The skin of the scale is made up of four superimposed, inverted, hollow, cup-like layers, the outer being the epidermis. Next to this is the oil droplet layer, then the leucophore layer, and lastly, the connective tissue layer which, however, supports the integrity of the whole.

The first and last named layers are continuous with those of the neighboring scales, but the second and third are limited to the scale.

The epidermis is a transparent layer which acts largely as a protecting and supporting structure and, through interference phenomena, acts slightly, if at all, as a factor in the color states.

The second or yellow oil droplet layer presents a thin transparent yellow medium which is extremely important in the production of many of the color states. In and superficial to it lie the fine terminals of the branches of the melanophores. The large zanthophores also lie in it and extend inward into the next layer. The oil droplets give a strong, bright color by transmitted light, but seem to reflect but little light (Fig. 10 A and B). It seems to act more as a filter than as a reflector. White light reflected from the underlying layer, when passing through this yellow medium, must be so acted upon as to give the yellow.

The leucophore layer, lying just internal to the oil droplet layer, acts essentially as a reflecting layer. It reflects a large proportion of the light which falls upon it, but it also screens the light to a great extent from the underlying brown melanophores so that pigment granules, when only in the bodies of the melanophores, exert but little influence on the color states of the skin. On the other hand, however, if the primary branches of the melanophores, which pierce this layer, are filled with pigment, the light which falls on it is reflected as blue light (Fig. 10 B). Further, cell bodies of the melanophores, lying internal to the leucophore layer, appear blue by reflected light in the scales of the ventral surface of the body in which the yellow oil droplet layer is very scant and in places absent (Fig. 7 B). Evidently then, the leucophore layer in part reflects all the rays of white light and also absorbs all but the blue rays from the light passing through it and reflected from the brown pigment within and internal to it. Traversing this leucophore layer are the large branches of the melanophores, connective tissue, and finer blood vessels. Partly imbedded in the lower stratum and beneath it are the melanophores. Fig. 17 is an attempt to show in perspective the various layers and their relation to one another.

The only layer that remains fixed and present in all scales and not subject to variations is the leucophore layer. All the other elements may be either absent, increased, decreased, or subject to marked variations. All of these other elements function in conjunction with the leucophore layer and either by allowing it to be unobscured, partially obscured, or by entirely shutting it off from the light, produce the color phenomena. The appearance of white and pale blue, as found on the ventral aspect of the body or along the mid-dorsal stripe, may be explained as due to the oil droplet layer being either absent or that it has been forced to the edges of the scale. A purely white scale must mean that the melanophores are either absent or greatly diminished in number, and very pale blue scales, that their pigment granules must have migrated entirely into the bodies of the cells. This allows the leucophore layer to act alone as a reflecting layer without the influence of any other element. In addition, the stratum corneum of the scales of the ventral surface is slightly thicker than in other regions, and this greater thickness, with the markedly developed keel of the scale found here, no doubt results in more light being reflected from the outer surface of the scale and thus a whiter appearance. It seems probable that by a vaso-dilatation of the superficial capillaries a pink color may be imparted to the white scales. Further, in addition to the blood capillaries, red pigment is manifestly present in the subcutaneous connective tissue of the throat-fan.

If, in the white scales, melanophores are present and send out pigment into the primary and larger branches, the light, which is now acted upon by the leucophore layer, is returned as blue. Decidedly blue scales are rare except in isolated scales on the lateral aspect of the body. Along the mid-dorsal stripe and on the ventral aspect, melanophores are too few in number to influence the color beyond a pale blue. I injected brown pigment (potassium bichromate solution) into the skin of the belly, and a blue color was readily produced. Higgins' brown ink furnishes the same result in the same way.

The yellow or orange appearance may be readily explained by the presence of the yellow oil droplet layer through which light from the leucophore layer must be transmitted. The melanophores, in the case of the yellow skin, must contain the pigment in their bodies, and the branches must be free of pigment. The degree of yellow color depends on the amount of oil droplets, the straw-yellow color being associated with a lesser amount than the deep yellow. Pale yellow is often present on the ventral aspect of some lizards due to the presence of a small amount of this substance.

The emerald green is brought about by the migration of pigment into the primary and larger branches of the melanophores. Now the light which is reflected from the leucophore layer, due to the presence of pigment granules, is blue, and this blue, in passing through the yellow oil droplet layer, mixes with yellow rays given by this layer and appears at the surface as green. By further distal migration of the pigment granules, light from the leucophore layer assumes a deeper blue which in turn produces the bluish-green color of the skin.

By a still more distal migration of the pigment a muddy, greenish gray appears which, as the migration proceeds, becomes brownish gray, then light brown and, lastly, a deep mahogany brown is produced, which indicates that distal migration has proceeded till the granules have accumulated immediately beneath the epidermis sufficiently to block the action of both the yellow oil droplets and the leucophore layer. The pigment granules now act entirely alone and produce the brown state (Figs. 12 and 13).

Whether the yellow oil droplet layer can be dispersed under varying stimuli in those scales where it normally exists, that is, whether it is possible for a lateral green scale to assume the white or bluish state in a short space of time, is difficult to say. If, as is held by Keller for the chameleon, the zanthophores possess the power of dilating and can take up all the space held previously by the oil droplet layer and thus displace the latter to the edges of the scale, it would at least be possible for a fairly rapid change to occur from green to white. Pouchet, however, believes the zanthophores of the chameleon to be of yellow color and if this be so, Keller's explanation would not be valid. The zanthophores of Anolis appear transparent in all the conditions under which I could observe them. They seem to be absent in the skin of the ventral surface of the body. However, my observations are by far too meager for me to draw any definite conclusions. It is true that the zanthophores seem greatly increased in the white scales of the mid-dorsal stripe and that they form a transparent fairly thick layer between the epidermis and the leucophore layer.

The objections to Keller's views are that if the zanthophores are able to disperse the oil droplet layer by dilating, they would probably also disturb the arrangement of the terminal branches of the melanophores, which we know does not take place. One would also conclude that these cells must be under the control of the nervous system. No conclusions can be reached without observing the living animals for long periods of time and noting the changes of these white areas. Possibly the white areas are merely variations and are more or less permanent. Black or brick-red stripes may be also variations in the distally migrated pigment.

The following table presents in a concise manner the mechanism involved in the various color states. Keller's theory in regard to the behavior of the zanthophores is included as a possibility, since their attributed function becomes necessary to explain white and blue changes in certain cutaneous areas, if these occur with any degree of rapidity.

TABLE 3

COLOR STATE	Oil Droplet Layer	Zantho-phore	Leuco-phore	Melano-phore	
White............	absent or dispersed	⊕ or absent	▭	●	
Blue.............	absent or dispersed	⊕ or absent	▭	◍ 1.	
Pink.............	absent or dispersed	⊕ or absent	▭	●	vaso-dilatation
Straw yellow......	partially dispersed	⊕ 2.	▭	●	
Golden yellow.....	▭	⊙ or absent	▭	●	
Emerald green....	▭	⊙ or absent	▭	◍ 1.	
Bluish green......	▭	⊙ or absent	▭	◍ 2.	
Grayish green.....	▥ 1.	⊙ or absent	▥ 1.	◍ 3.	
Brownish green....	▥ 2.	⊙ or absent	▥ 2.	◍ 4.	
Light brown......	▥ 3.	⊙ or absent	▥ 3.	◍ 5.	
Mahogany brown..	■	⊙ or absent	■	○	brown pigment granules
Brick-red.........	■	⊙ or absent	■	○	brick-red pigment granules
Black............	■	⊙ or absent	■	○	black pigment granules

▭ unobstructed, ▥ partially obscured, ■ obscured, ⊕ dilatation of zanthophore, ⊙ contraction of zanthophore, ○ maximum distal migration of pigment, ◍ partial distal migration of pigment, ● maximum proximal migration of pigment. No. 1-5 indicate comparative degrees of either obscuration or migration.

For the final solution of this problem of the color changes in Anolis, three methods of attack must be carried on and one must not lose sight of any one of them: Carefully controlled physiological experiments, histological studies of the skin, and careful observations over long periods of time of the habits and color states of these lizards in their natural environment. The first method of attack is always open to criticism so long as the experiments are not carefully controlled; for instance in none of the experiments performed by either Parker and Starratt or Carlton were the factors of varying external stimuli taken into consideration.

Lizards kept for long periods in confinement may give one set of results but one is not justified in drawing any general conclusions as to the behavior of all lizards.

I wish to thank Doctor Hardesty and Doctor Garey for their helpful suggestions.

Summary

1. In its color changes, *Anolis carolinensis* shows a greater variety of colors than has been usually described for this animal. It may at times take on other colors than the emerald green, mahogany brown, and the variations intermediate between these. The variations, though apparently less frequent, correspond fairly closely with the variations described for *Chamæleon vulgaris*.

2. The color changes, in addition to general variations in *Anolis carolinensis*, as observed in its natural environment especially, seem to be induced by variations in external stimuli. Rhythmic changes of color may be observed with the animal in the same position with unchanged temperature and light, and emotional states interpreted as fear, sexual excitement, and anger (preliminary to and during combat) seem to more actively bring about color changes than temperature and light. Color changes in sympathy with environment (protective coloration) seem probable.

3. In structure, the skin of Anolis resembles that described by other investigators for *Chamæleon vulgaris*, except no "Negative Relief Schicht" could be distinguished in the stratum corneum of the epidermis, and no cells corresponding exactly to the erythrophores of Pouchet could be determined. Also the oil droplet layer described here for Anolis is not the same as the ochrophore layer described by Keller for Chamæleon.

4. The observations of Carlton that the processes of the melanophores in Anolis are fixed or non-amœboid and that migration of the pigment granules occurs within them, is hereby confirmed. In this the melanophores are similar to those described for

Chamæleon, *Fundulus heteroclitus*, *Rana temporaria*, and other color-changing animals.

5. The color changes in Anolis depend upon the reciprocal physical action of four layers of the skin: the epidermis, the yellow oil droplet layer, the leucophore layer and the melanophores. The physical characters making possible light interference and absorption, and the mixing of transmitted and reflected rays, modified by the migration of pigment to different positions in these layers, result in the varieties of color apparent at the surface of the skin at different times and on different localities of the body. The red coloration of the throat-fan is due to a rich capillary plexus and to the presence of a red coloring matter in the deeper layers. The effect of vaso-dilatation is also apparent in the pink stripe noted occasionally along the mid-dorsal line.

6. The oil droplet layer and the leucophore layer in general remain fixed and the various color states depend on the migration of the pigment granules in the fixed processes of the melanophores. Maximal proximal migration of the pigment is associated with yellow, while maximal distal migration produces dark mahogany brown. In the emerald green state the pigment lies in the primary and larger branches of the melanophores. Further distal migration is associated with bluish-green or slaty-gray color states depending on the degree.

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Description of Plates

Plate 7, Figs. 1-5

Camera-lucida outlines of scales of various parts of the body.

Plate 8, Fig. 6

(A). External surface of the skin of the lateral aspect under low power by transmitted light, showing yellow scales and indistinct melanophores (M).

(B). The same as above by reflected light showing the green scales with areas of brown pigmentation.

(C). Internal surface of the same skin by reflected light showing the blue scales with distinct dark melanophores (M).

Plate 8, Fig. 7

(A). External surface of the skin of the ventral aspect under low power by transmitted light showing the pale straw-colored scales with their indistinct melanophores (M).

(B). the same as above by reflected light showing the white scales with indistinct blue melanophores (M).

(C). Internal surface of the same by transmitted light showing the straw-colored scales with their distinct melanophores.

Plate 7, Fig. 8

Vertical section of a portion of the ventral scale (oil immersion) showing the stratum corneum (st. corn.), stratum germinativum (st. germ.), the leucophore layer (leuc.), a single melanophore (melan.), and the connective tissue (conn. tiss.).

Plate 7, Fig. 9

Scraping of the stratum corneum under oil immersion showing a group of squamous cells with their stippled appearance.

Plate 9, Fig. 10 (High Dry Power)

(A). Vertical section of a lateral scale in the green state by transmitted light, freshly hardened with twenty per cent formalin and unstained. This shows the transparent epidermis, the underlying layer of yellow oil droplets (O), the layer of leucophores (L), the melanophores with their numerous branches (M), and the underlying layer of connective tissue (C).

(B). The same by reflected light showing the bluish-white leucophore layer (L) and the black melanophores (M). The latter appear blue when lying beneath the former. The yellow oil droplet layer scarcely reflects any light.

Plate 9, Fig. 11 (Oil immersion)

Vertical section of a lateral scale in the green state, stained with haemotoxylin and eosin showing the various layers of the epidermis and corium. Small amounts of pigment appear in the terminal branches of the melanophores but the mass appears in the cell bodies.

Plate 9, Fig. 12 (Oil immersion)

Vertical section of a lateral scale in the brown state stained with haemotoxylin and eosin showing the pigment lying just beneath the epidermis.

Plate 9, Fig. 13 (Oil immersion)

Vertical section of a dorso-lateral scale in the brown state stained with haemotoxylin and eosin showing the pigment cells (P) and a blood vessel, lying just beneath the connective tissue layer, sending a branch through all the layers and which ends just beneath the epidermis. The leucocytes are evident.

Plate 9, Fig. 14 (Oil immersion)

Tangential section of a lateral scale in the brown state showing the pigment in the terminal branches of the melanophores (T), the pigment just beneath the epidermis (E), the leucophores with their bizarre outlines (L), the secondary branches of the melanophores piercing the openings between the melanophores (S), and the bodies of the melanophores with their primary branches (M).

Plate 8, Fig. 15 (Oil immersion)

(A). Melanophores occasionally found showing a central migration of the pigment in the body of the cell, forming a rounded mass surrounded by a halo of clear cytoplasm.

(B). Melanophores frequently found showing an almost complete proximal migration of the pigment. Practically no pigment exists even in the primary branches. The nuclei are evident.

Plate 9, Fig. 16 (Oil immersion)

Pigment cell seen from above. These cells are found in the spaces between the scale and throughout the entire body. In vertical section these cells appear flat.

Plate 7, Fig. 17

Reconstruction of the skin of *Anolis carolinensis* showing the essential elements necessary for the production of the color states, namely, the epidermis, yellow oil droplet layer, zanthophores, leucophores, and melanophores.